Genet. Res., Camb. (2002), **79**, *pp.* 49–63. *With* 4 *figures.* © 2002 Cambridge University Press
DOI: 10.1017/S0016672301005407 Printed in the United Kingdom

Chromosomal inversion polymorphism in Afrotropical populations of *Drosophila melanogaster*

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(*Received 2 May 2000 and in revised form 12 September 2001*)

Summary

When 41 populations from Africa (south of the Sahara) and Indian Ocean islands were analysed for their chromosomal inversion polymorphism, 34 rearrangements were found, including the four common cosmopolitans (*In(2L)t*, *In(2R)NS*, *In(3L)P* and *In(3R)P*), four rare cosmopolitans (*In(2L)NS*, *In(3R)C*, *In(3R)Mo* and *In(3R)K*) and six African polymorphic ('recurrent') endemics. Mean inversion frequencies per major autosome arm were positively and, generally, highly correlated to each other. There was no altitudinal nor latitudinal cline of inversion frequency, except for one African polymorphic endemic. Significant longitudinal clines were detected for *In(2L)t*, *In(3L)P* and *In(3R)K*; in all cases, inversion frequencies decreased eastward. Principal components analysis and ANOVA made it possible to distinguish three groups of populations. A high level of polymorphism was found in populations from west tropical Africa. The other low altitude populations from the mainland were moderately polymorphic, whereas the lowest levels of polymorphism were those of high altitude populations and of Indian Ocean islands. Moreover, some regional and local differentiation was also found. The frequency of unique autosomal inversions was not different from those found in Asia, Australia and America, but was significantly higher than that in Europe and North Africa. A West–East differentiation was also observed for the African polymorphic endemics. The present geographic pattern suggests a long, patchy evolution with restricted gene flow, followed by the modern period with numerous recent migrations linked to human transportation.

1. Introduction

After the beginning of formal genetic investigations of *Drosophila melanogaster*, the geographic origin of that species long remained a mystery. Moreover, this cosmopolitan, domestic species was generally considered of little evolutionary interest because of its stable, man-linked ecological niche. During the past few decades, it has been suggested, and eventually confirmed, that *D. melanogaster* originated from tropical Africa (Tsacas & Lachaise, 1974; Lachaise *et al.*, 1988; David & Capy, 1988). Two kinds of argument are generally given for assuming an African origin of *D. melanogaster*. First, of the nine related species belonging to the monophyletic *D. melanogaster* subgroup (Lemeunier *et al.*, 1986; Lachaise *et al.*, 2000), seven are endemic to Africa. Second, African populations are generally found to be more polymorphic than populations from other parts of the world (Singh *et al.*, 1982; Daïnou *et al.*, 1987; David and Capy, 1988), the more recent evidence coming from molecular analyses of different African populations (Begun & Aquadro, 1993; Bénassi *et al.*, 1993; Bénassi, 1994; Bénassi & Veuille, 1995). Furthermore, it has been suggested that some African populations might be in a process of incipient speciation (Wu *et al.*, 1995). This would indicate that the presence of *D. melanogaster* is not recent, supporting the antiquity of this species in Africa.

Among different types of genetical markers, chromosome rearrangements are especially interesting for two main reasons. First, polymorphic inversions have unique origins (Inoue, 1979a; Sperlich & Pfriem, 1986; Inoue & Watanabe, 1992; Krimbas & Powell, 1992; Wesley & Eanes, 1994; Powell, 1997; Andolfatto

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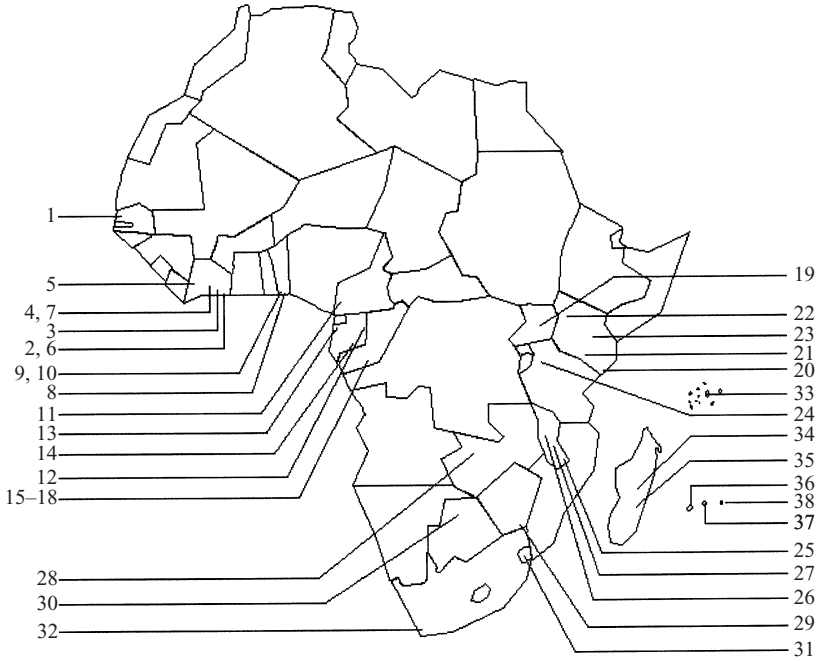

Fig. 1. Geographical locations of the *D. melanogaster* African samples. Numbers refer to localities listed in Appendix 1.

et al., 1999). An inversion can thus be considered to be an excellent historical marker. Second, because genes included in an inversion do not recombine with the *Standard* sequence, with the exception of rare double crossovers, functional co-adaptations are likely to occur within an inversion, so that rearrangements might also be involved in adaptive polymorphism (Dobzhansky, 1950).

Since the pioneer cytological study carried out in the USSR (Dubinin *et al*., 1937), more than 500 different rearrangements have been described (Lemeunier & Aulard, 1992). Thus, *D. melanogaster* appears to be a highly variable species with respect to its chromosomal sequences. Depending on their geographical distribution and their frequencies, these inversions have been classified as cosmopolitan (common and rare) and endemic (recurrent and unique) (Ashburner & Lemeunier, 1976; Mettler *et al*., 1977); recurrent inversions are described as 'polymorphic endemics' by Inoue & Igarashi (1994). Strong support for the adaptive nature of certain gene arrangements comes from a variety of observations: latitudinal clines of inversion frequencies, in North America, Australia and Asia (Stalker, 1976; 1980; Mettler *et al*., 1977; Voelker *et al*., 1977; 1978; Inoue & Watanabe, 1979; Yamaguchi *et al*., 1980; Knibb *et al*., 1981; Knibb, 1982; Inoue *et al*., 1984; Anderson *et al*., 1987; Das & Singh, 1991; Singh & Das, 1992); heterokaryotype superiority (Watanabe, 1969; Watanabe & Watanabe, 1973; Watanabe *et al*., 1976; Stalker, 1976; Inoue, 1979a); seasonal cyclic fluctuations, in North America, Australia, Asia and Europe (Inoue, 1979b; Stalker, 1980; Masry, 1981; Inoue *et al*., 1984; Knibb, 1986; Sanchez-Refusta *et al*., 1990); and gametic disequilibria (references in Lemeunier & Aulard, 1992).

Surprisingly, and in spite of their major interest, Afrotropical populations have been poorly investigated for their chromosomal polymorphism and, in many cases, only qualitative data are available. The present study was undertaken to answer two general related questions. (1) Are these ancestral populations more polymorphic than the derived populations found in Eurasia, America and Australia? (2) Do rearrangements in Africa exhibit geographic trends similar to those observed in the rest of the world? Several original conclusions can be drawn from our investigation, including the existence of a large degree of heterogeneity among Afrotropical populations, some micro- and macrogeographic trends, the occurrence of several polymorphic endemic ('recurrent') inversions, and a general pattern quite different from that found in other parts of the world.

2. Materials and methods

(i) Drosophila *strains*

Wild *D. melanogaster* were collected in 20 populations from West, East and South Africa (south of the Sahara) and from Indian Ocean islands. Inseminated females were used to initiate isofemale lines. Geographical origins and dates of collection are listed in Appendix 1. In addition to these samples, previous data on African populations are also considered. The geographical position of the whole set of 38 localities is shown in Fig. 1.

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(ii) *Cytological analyses*

Wild males from nature or a single male from each isofemale line (no more than 10 generations after its establishment) were crossed individually to virgin Canton-S females homozygous for the *Standard* chromosome sequence (*St*). A salivary gland preparation was made from a single 3rd-instar female larva from each cross. Breakpoints were determined by comparing photographs with the standard maps of Lefevre (1976) and Sorsa (1988). When identical endemic inversions had been detected in different isofemale lines, larvae from these lines were directly analysed to confirm that the inversions were not carried by the Canton-S chromosomes themselves.

(iii) *Statistical analyses*

Simple correlations and multiple regressions of angularly transformed inversion frequencies on altitude, latitude and longitude were analysed. In the analyses, northerly and southerly latitudes were both given positive values and hence represent distances from the equator. However, longitude was signed, with locations east of Greenwich positive and those west negative; distance from the meridian of Greenwich is simply used as a geographical distance. The data were also submitted to a principal components analysis, which revealed the existence of three groups of populations.

3. Results

(i) *Chromosome rearrangements*

From all populations sampled, 34 different rearrangements have been identified. Their nature, their number and, for the endemic sequences, the populations in which they were found are given in Appendix 2.

(a) *Cosmopolitan inversions*

All four common (*In(2L)t*, *In(2R)NS*, *In(3L)P* and *In(3R)P*) and four rare (*In(2L)NS*, *In(3R)C*, *In(3R)Mo* and *In(3R)K*) were identified.

(b) *Endemic sequences*

Six of the 26 endemic rearrangements are rarely found in nature, presumably because of their deleterious effects: two deficiencies (numbers 6 and 29) and four pericentric inversions on chromosome 2 (numbers 16–19). Two of the 2R inverted sequences (numbers 8 and 10) are complex, with included (52C;53E in 43B;54E) and overlapping (44F3-12;54E3-10 + 51B6-11;55E3-12) inversions. Six inversions (numbers 1–3, 12, 18 and 20) are polymorphic, because they have been found in different, distant populations and in many cases reached frequencies above 1% (Table 1); some of them have persisted over several years in the same natural population. Two of these recurrent inversions are on the X chromosome (numbers 1 and 2) and one is pericentric on chromosome 2 (number 18). In *D. melanogaster*, as in other species, X-linked inversions are rare in nature because of their possible deleterious effects in hemizygous males. This is also true for pericentric inversions because of aneuploid eggs produced by recombination in female heterokaryotypes. These are the first known examples of X and pericentric inversion polymorphism in natural populations of *D. melanogaster* (Aulard, 1990; Coyne *et al.*, 1991; Eanes *et al.*, 1992). More detailed comments about these six inversions are given in Lemeunier and Aulard (1992). They are abbreviated as *In(1)A*, *In(1)Be*, *In(2L)IC*, *In(2R)Ca*, *In(2LR)PL* and *In(3L)Ok*, respectively (Fig. 2). Their geographical distribution is shown in Fig. 3.

(ii) *Polymorphism at the inversion level*

Frequencies of cosmopolitan and polymorphic endemic inversions are given in Table 1. In some samples, cosmopolitan inversions are more frequent than the *Standard* sequences, for example *In(2L)t* in Tai (0·50 and 0·52), in Lamto (0·64 and 0·61) and Cotonou (0·64), or *In(3R)P* in Tai (0·64 and 0·53). In order of decreasing mean frequency (Table 2), the cosmopolitan inversions can be classified as follows.

$$In(2L)t > In(3R)K > In(3R)P > In(3L)P > In(2R)NS > In(3R)C > In(3R)Mo > In(2L)NS$$

The highest mean frequency is observed for *In(2L)t*, which is also the most widespread inversion, being found in 70% of the samples (Table 2). *In(3R)K*, classified as rare cosmopolitan or 'quasi-cosmopolitan' (Inoue & Igarashi, 1994) because of its restricted geographical distribution and its usually low frequency on other continents, is widely distributed in the Afrotropical region. It has been found in 66% of the sites, at a frequency sometimes higher than that of common cosmopolitan inversions. It was almost the only inversion found at Mt Elgon (Kenya), at a frequency of 0·48 (Table 1). Unlike *In(3R)K*, *In(2L)NS* and *In(3R)Mo* are very restricted in their distributions and frequencies.

The polymorphic endemic inversions are less widely distributed than the cosmopolitans but their frequencies, which vary greatly between populations, can reach 33% (*In(3L)Ok* in Zambia, Table 1). Among them, *In(2R)Ca*, with a mean frequency of 0·02 and a presence in 22% of the samples (Table 2), is the most widespread.

Finally, taking into account their mean frequency (above 0·01) and their distribution (present in > 20% of the samples) (Tables 1, 2), we consider that seven inversions (*In(2L)t*, *In(2R)NS*, *In(3L)P*, *In(3R)P*,

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Table 1 *Frequencies of cosmopolitan* (*A*) *and polymorphic endemic* (*B*) *inversions found in African samples*
(A) Cosmopolitan inversions

Populations (Ref.)	*N*	*In(2L)t*	*In(2L)NS*	*In(2R)NS*	*In(3L)P*	*In(3R)P*	*In(3R)K*	*In(3R)C*	*In(3R)Mo*
Dakar (e)	74	0·405	0·000	0·081	0·405	0·000	0·135	0·000	0·000
Abidjan (g)	*	+	−	+	+	+	−	−	−
Agboville (g)	*	+	−	−	+	+	+	−	−
Bouake (g)	*	+	−	−	−	+	+	−	−
Tai, 1981 (a)	42	0·500	0·000	0·119	0·381	0·643	0·214	0·000	0·000
Tai, 1983 (a)	75	0·520	0·000	0·080	0·173	0·533	0·387	0·000	0·000
Adiopodoume (a)	*	+	−	−	−	+	+	−	−
Lamto, 1984 (a)	33	0·636	0·000	0·121	0·242	0·333	0·333	0·061	0·000
Lamto, 1989 (c)	83	0·614	0·024	0·205	n.a.	n.a.	n.a.	n.a.	n.a.
Porto Novo (g)	*	−	−	−	−	−	−	−	−
Cotonou (a)	36	0·639	0·000	0·111	0·333	0·306	0·278	0·194	0·000
Djeffa (a)	29	0·138	0·000	0·034	0·069	0·000	0·310	0·000	0·000
Kumba (g)	*	−	−	−	−	+	+	−	−
Belinga (g)	*	−	−	−	−	+	+	−	−
Libreville (g)	*	+	−	−	−	+	+	−	−
Makokou (g and a)	*	+	−	−	−	+	+	−	−
Loua (a)	60	0·083	0·000	0·050	0·083	0·100	0·050	0·033	0·000
Brazzaville (a)	42	0·190	0·000	0·024	0·119	0·143	0·262	0·167	0·000
Brazza–Kron (a)	18	0·000	0·000	0·000	0·000	0·000	0·055	0·000	0·000
Loukanga (a)	19	0·000	0·000	0·000	0·000	0·000	0·000	0·000	0·000
Kampala (g)	*	−	−	−	−	−	+	−	−
Mombasa (f)	*	−	−	−	−	−	−	−	−
Nairobi (f)	54	0·185	0·000	0·000	0·019	0·074	0·056	0·037	0·000
Mt Elgon (a)	21	0·000	0·000	0·000	0·000	0·048	0·476	0·000	0·000
Mt Kenya (f)	30	0·267	0·000	0·000	0·000	0·000	0·033	0·000	0·000
Nyengesi (a)	*	−	−	−	−	−	−	−	−
Limbe (g)	*	−	−	−	−	−	−	−	−
Kasungu (b)	50	0·200	0·000	0·040	n.a.	n.a.	n.a.	n.a.	n.a.
Lilongwe (b)	12	0·167	0·000	0·000	n.a.	n.a.	n.a.	n.a.	n.a.
Luangwa (d)	86	0·244	#	0·233	0·000	0·035	0·000	0·000	0·000
Mt Silinda (g)	*	+	−	−	−	−	−	−	−
Okavango (d)	71	0·352	#	0·099	0·000	0·197	0·000	0·000	0·000
Mbuluzi (a)	9	0·222	0·000	0·111	0·000	0·000	0·444	0·111	0·000
Cape Town (a)	26	0·154	0·000	0·038	0·000	0·038	0·038	0·154	0·115
Mahe (a)	34	0·176	0·000	0·088	0·000	0·235	0·000	0·059	0·000
Tananarive (f)	26	0·269	0·000	0·000	0·000	0·000	0·000	0·038	0·000
Ranomafana (a)	35	0·286	0·000	0·000	0·000	0·000	0·086	0·000	0·000
St Denis (g)	*	+	−	−	+	+	+	−	−
Port Louis (a)	30	0·000	0·000	0·000	0·000	0·000	0·000	0·000	0·000
Port Mathurin (a)	14	0·000	0·000	0·000	0·000	0·000	0·000	0·000	0·000

(B) Polymorphic endemic inversions

Populations (Ref.)	*N*	*In(1)A*	*In(1)Be*	*In(2L)IC*	*In(2R)Ca*	*In(2LR)PL*	*In(3L)Ok*
Dakar (e)	74	0·000	0·000	0·000	0·000	0·000	0·000
Abidjan (g)	*	−	−	−	−	−	−
Agboville (g)	*	−	−	−	−	−	−
Bouake (g)	*	−	−	+	−	−	−
Tai 1981 (a)	42	0·000	0·048	0·000	0·214	0·000	0·000
Tai 1983 (a)	75	0·000	0·013	0·000	0·013	0·000	0·000
Adiopodoume (a)	*	−	+	−	−	−	−
Lamto, 1984 (a)	33	0·000	0·000	0·000	0·091	0·000	0·000
Lamto, 1989 (c)	83	n.a.	n.a.	0·000	0·024	0·000	n.a.
Porto Novo (g)	*	−	−	+	−	−	−
Cotonou (a)	36	0·000	0·139	0·000	0·139	0·000	0·000
Djeffa (a)	29	0·000	0·000	0·000	0·034	0·000	0·000
Kumba (g)	*	−	−	−	+	−	−
Belinga (g)	*	−	−	−	−	−	−
Libreville (g)	*	−	−	−	−	−	−
Makokou (g and a)	*	−	−	−	+	−	−
Loua (a)	60	0·000	0·000	0·000	0·000	0·000	0·000

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Table 1 (*cont.*)
(B) Polymorphic endemic inversions (*cont.*)

Populations (Ref.)	*N*	*In(1)A*	*In(1)Be*	*In(2L)IC*	*In(2R)Ca*	*In(2LR)PL*	*In(3L)Ok*
Brazzaville (a)	42	0·000	0·048	0·000	0·048	0·000	0·000
Brazza–Kron (a)	18	0·000	0·111	0·000	0·000	0·000	0·000
Loukanga (a)	19	0·000	0·000	0·000	0·000	0·000	0·000
Kampala (g)	*	–	–	–	–	–	–
Mombasa (f)	*	–	–	–	–	–	+
Nairobi (f)	54	0·000	0·000	0·000	0·000	0·000	0·000
Mt Elgon (a)	21	0·000	0·000	0·000	0·000	0·000	0·000
Mt Kenya (f)	30	0·000	0·000	0·000	0·000	0·000	0·000
Nyengesi (a)	*	+	–	–	–	–	–
Limbe (g)	*	–	–	–	–	–	+
Kasungu (b)	50	n.a.	n.a.	0·000	0·000	0·000	n.a.
Lilongwe (b)	12	n.a.	n.a.	0·000	0·000	0·000	n.a.
Luangwa (d)	86	0·116	0·000	0·000	0·000	0·000	0·326
Mt Silinda (g)	*	–	–	–	–	–	–
Okavango (d)	71	0·127	0·000	0·000	0·000	0·000	0·225
Mbuluzi (a)	9	0·000	0·000	0·000	0·000	0·000	0·000
Cape Town (a)	26	0·000	0·038	0·000	0·000	0·000	0·000
Mahe (a)	34	0·000	0·000	0·000	0·029	0·000	0·000
Tananarive (f)	26	0·000	0·000	0·000	0·000	0·000	0·000
Ranomafana (a)	35	0·000	0·000	0·000	0·000	0·000	0·000
St Denis (g)	*	–	–	+	–	–	–
Port Louis (a)	30	0·000	0·000	0·033	0·000	0·033	0·000
Port Mathurin (a)	14	0·000	0·000	0·071	0·000	0·071	0·000

When only qualitative data are available (*), presence of inversions is shown by '+'.
Abbreviations: n.a., non analysed; *N*, number of haploid genomes; #, two observations were made in Luangwa and/or Okavango; *In(1)A*, *In(1)12A;18D*; *In(1)Be*, *In(1)16D;18D*; *In(2L)IC*, *In(2L)22A;26B*; *In(2R)Ca*, *In(2R)49B;56A*; *In(2LR)PL*, *In(2LR)31F;51C*; *In(3L)Ok*, *In(3L)62DE;68A*.
References: a, present study; b, Bénassi, 1994 (data only for chromosome 2); c, Bénassi *et al.*, 1993 (data only for chromosome 2); d, Eanes *et al.*, 1992; e, Afonso *et al.*, 1985; f, Inoue & Watanabe, 1980; g, Ashburner & Lemeunier, 1976.

In(3R)K, *In(3R)C* and *In(2R)Ca*) are the most widespread and polymorphic in Africa and will be referred thereafter as 'African polymorphic inversions'.

The mean inversion frequencies per major autosome arm (all inversions are considered) are all positively and significantly correlated with each other (Table 3A). This implies that, when a chromosome arm shows a high inversion frequency, this is also true for the others. These observations are mostly due to the four common cosmopolitan inversions *In(2L)t*, *In(2R)NS*, *In(3L)P* and *In(3R)P*, whose frequencies are positively and significantly correlated with each other and with the recurrent *In(2R)Ca*. Correlations involving *In(3R)C* and *In(3R)K* are also positive but are significant only for *In(3R)K* correlated with *In(3L)P* and *In(2R)Ca* (Table 3B).

The amount of genetic differentiation among populations was estimated by the fixation index *Fst* (Wright, 1951). Values (Table 2) ranged from 0·08 to 0·26 for the common cosmopolitans (average 0·19), from 0·1 to 0·22 for the rare cosmopolitans (average 0·14) and from 0·06 to 0·28 for the polymorphic endemics (average 0·11). There is no difference between the three kinds of inversion, which exhibit similar amounts of geographic variation. The overall value of *Fst* ($0{\cdot}143 \pm 0{\cdot}022$) is very high, showing that African populations are not homogeneous. The spatially structured pattern is further analysed below.

(iii) *Geographical pattern of African polymorphic inversions*

Variation between populations was also investigated by considering its relationship with the geographical parameters altitude, latitude and longitude. Analyses were carried out for the seven widespread African inversions. Data from Lamto (1989), Lilongwe and Kasungu were excluded because only chromosome 2 was analysed; the two samples from Tai were pooled. Given the distance between Loua and Loukanga (< 2 km), and the similarities of the breeding sites (peelings of manioc), these two samples were also pooled. Results are given in Table 4 in terms of simple correlation (r) and multiple regression (b) coefficients. For the cosmopolitan inversions, a significant correlation with altitude or latitude was never found, even after multiple regression analyses. By contrast, with the exception of *In(3R)P* and *In(3R)C*, significant correlations with longitude were revealed for the four other cosmopolitan inversions. All correla-

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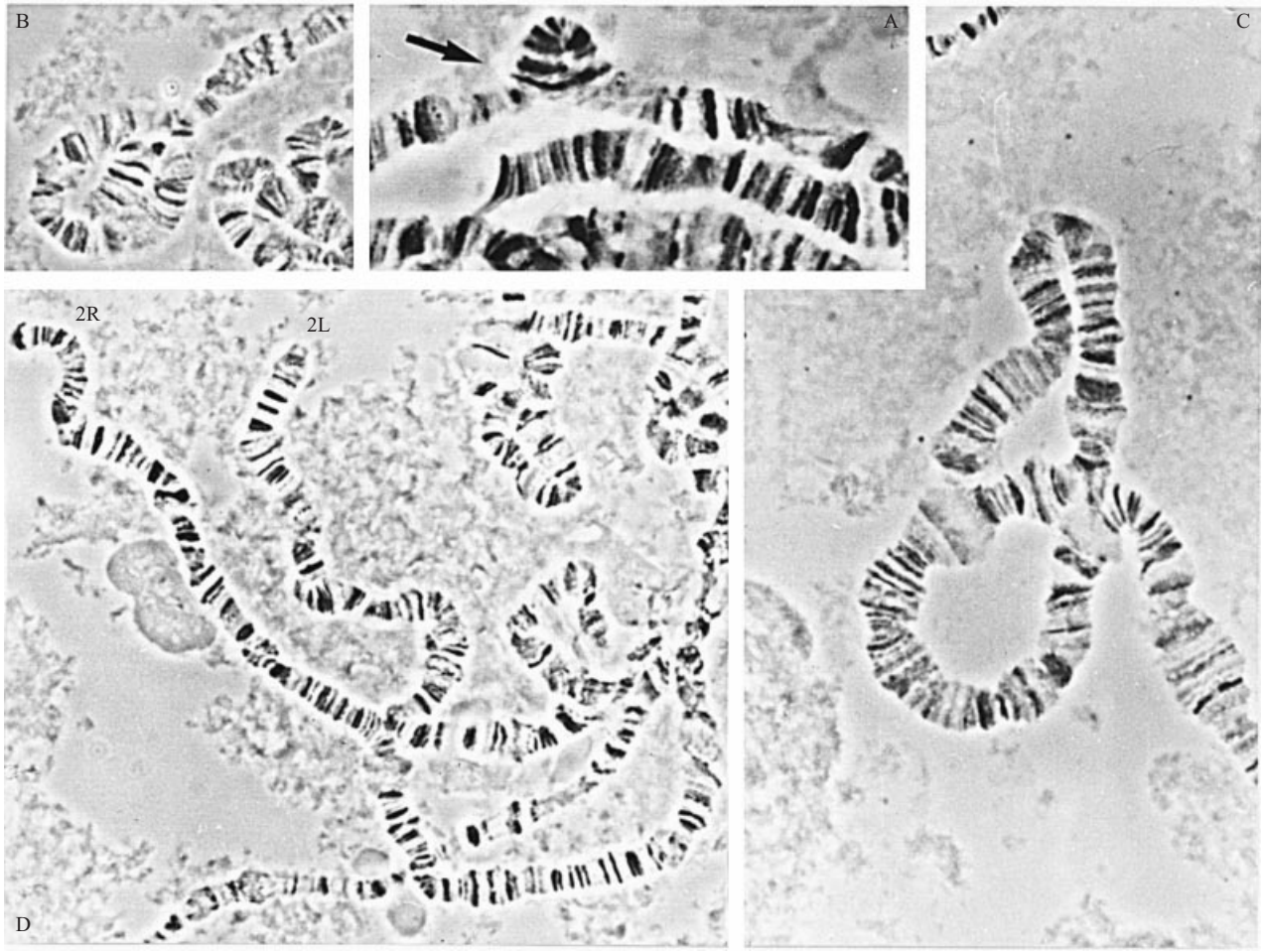

Fig. 2. Polymorphic endemic inversions found in the African populations of *D. melanogaster*. A, *In(1)Be* = *In(1)16D;18D* (from Aulard, 1990); B, *In(2L)IC* = *In(2L)22A;26B*; C, *In(2R)Ca* = *In(2R)49B;56A*; D, *In(2LR)PL* = *In(2LR)31F;51C* (from Aulard, 1990).

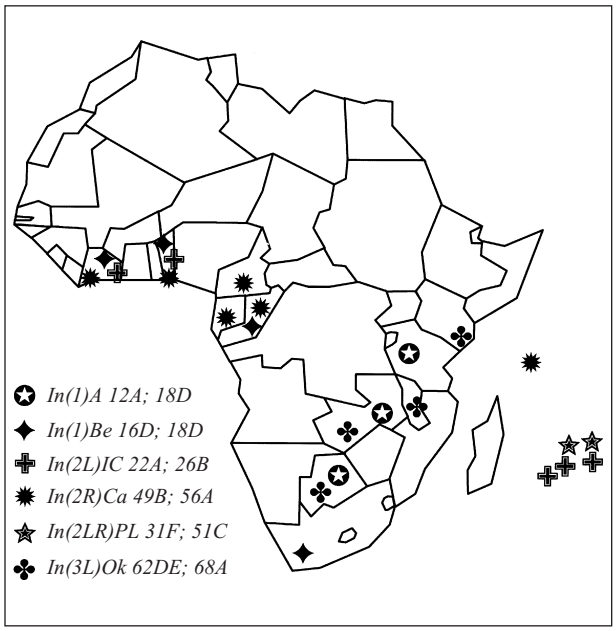

Fig. 3. Geographical distribution of the polymorphic endemic inversions in the African populations.

tions are negative, showing an eastward decrease in inversion frequencies. The existence of such longitudinal clines was corroborated, except for *In(2R)NS*, after correcting for altitude and latitude. The greatest effect was for *In(3L)P*, with 74% of total variation explained. For the two others, longitude accounted for 36%, on average, of the geographic variability. Multiple regression analyses revealed significant altitudinal and latitudinal clines for *In(2R)Ca*, the frequency decreasing with altitude and increasing distance from the equator.

In order to determine which inversions are involved in the distribution of these populations, a principal components analysis was carried out (Fig. 4). Correlation between variables and principal components revealed that the four common cosmopolitans and the 2R polymorphic endemic were highly correlated with axis 1 (correlations of 0·803, 0·689, 0·802, 0·796 and 0·882 for *In(2L)t*, *In(2R)NS*, *In(3L)P*, *In(3R)P* and *In(2R)Ca*, respectively), whereas *In(3R)K* and *In(3R)C* were less informative (0·559 and 0·521, respectively). Thus, populations with high frequencies of *In(2L)t*, *In(2R)NS*, *In(3L)P*, *In(3R)P* and

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Table 2. *Analysis of non-unique inversions in Afrotropical populations*

	A			B	
Inversions	*N*	Mean frequency	*Fst*	*N*	%
Common cosmopolitan					
*In(2L)t**	22	0·231 ± 0·039	0·192	37	70·3
*In(2R)NS**	22	0·053 ± 0·014	0·083	37	37·8
*In(3L)P**	20	0·075 ± 0·028	0·229	35	31·4
*In(3R)P**	20	0·102 ± 0·034	0·255	35	57·1
Rare cosmopolitan					
In(2L)NS				37	8·1
*In(3R)K**	20	0·144 ± 0·036	0·216	35	65·7
*In(3R)C**	20	0·042 ± 0·014	0·097	35	25·7
In(3R)Mo	20	0·006 ± 0·006	0·111	35	2·9
Polymorphic endemic					
In(1)A	20	0·012 ± 0·008	0·116	35	8·6
In(1)Be	20	0·018 ± 0·009	0·087	35	17·1
In(2L)IC	22	0·005 ± 0·003	0·056	37	13·5
*In(2R)Ca**	22	0·017 ± 0·008	0·075	37	21·6
In(2LR)PL	22	0·005 ± 0·003	0·056	37	5·4
In(3L)Ok	20	0·028 ± 0·019	0·280	35	11·4

A, Mean frequency of each inversion with standard error in populations for which frequency data are available. B, percentage of populations harbouring a given inversion.
Abbreviations: *Fst*, fixation index among populations; *N*, number of samples; *, marked inversions were found in > 20% of the samples and are referred as 'African polymorphic inversions'.
Samples from Tai (1981 and 1983), from Lamto (1984 and 1989) and from Loua and Loukanga were pooled (i.e. three pools).

In(2R)Ca are projected to the right whereas low polymorphic populations are found in the left (Fig. 4, bottom). The dispersion of these populations on axis 2 is due to *In(3R)K*. These observations are corroborated by the correlations between the cosmopolitan and the 2R polymorphic endemic inversions frequencies (Table 3B). *In(2L)t*, *In(2R)NS*, *In(3L)P*, *In(3R)P* and *In(2R)Ca* were significantly and, on the whole, highly correlated with each other, whereas correlations involving *In(3R)K* and *In(3R)C* were slightly or not significant. From this analysis, three groups of populations, well differentiated on axis 1, could be observed and they were defined as follows.

(1) AFH (high polymorphism): Tai and Lamto (the Ivory Coast), and Cotonou (Benin).
(2) AFM (moderate polymorphism): Dakar (Senegal), Djeffa (Benin), Brazzaville and Loua–Loukanga (Congo), Luangwa (Zambia), Okavango (Botswana), Mbuluzi (Swaziland), Cape Town (South-Africa), and Mahe (the Seychelles).
(3) AFL (low polymorphism): Brazzaville-Kronenbourg (Congo), Nairobi, Mt Elgon and Mt Kenya (Kenya), Tananarive and Ranomafana (Madagascar), Port Louis (Mauritius), and Port Mathurin (Rodrigues).

This grouping was corroborated by an ANOVA (not shown): between-groups variability was more important than within-group variability, and differences were highly significant for all four common cosmopolitans and for the polymorphic endemic *In(2R)Ca*.

(iv) *World frequency of unique endemic inversions*

Data from publications on naturally occurring inversions were compiled in order to estimate the frequency of the autosomal endemic rearrangements in different geographic regions of the world. This literature was difficult to review for several reasons. First, some authors focused only on polymorphic inversions and did not mention the endemics. Second, breakpoints of endemics were often not determined, and these

Table 3. *Correlations between inversion frequencies*
A

(*N* = 22)	2L	2R	3L
2R	0·626**		
3L	0·644***	0·727***	
3R	0·558**	0·539**	0·527*

B

(*N* = 22)	*In(2L)t*	*In(2R)NS*	*In(3L)P*	*In(3R)P*	*In(3R)K*	*In(3R)C*
In(2R)NS	0·654***					
In(3L)P	0·650***	0·481*				
In(3R)P	0·611**	0·585**	0·594**			
In(3R)K	0·356	0·237	0·529*	0·344		
In(3R)C	0·313	0·253	0·174	0·219	0·243	
In(2R)Ca	0·574**	0·464*	0·722***	0·735***	0·437*	0·330

A, Correlations between chromosome arms. B, Correlations between the seven African polymorphic inversions. Frequencies were angularly transformed. Samples from Lamto (1989), Kasungu and Lilongwe were excluded from the analysis.
Abbreviations: *, $p < 0{\cdot}05$; **, $p < 0{\cdot}01$; ***, $p < 0{\cdot}001$; *N*, number of populations.

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Table 4. *Correlation and regression analyses of frequencies with altitude, latitude and longitude*

	Simple (*r*)			Multiple (*b*)			
Inversions	Altitude	Latitude	Longitude	Altitude	Latitude	Longitude	R^2
In(2L)t	−0·132	−0·045	−0·551*	$+1{\cdot}0\times10^{-4}$	+0·0090	−0·0157*	0·323
In(2R)NS	−0·434	+0·063	−0·507*	$-1{\cdot}2\times10^{-4}$	+0·0030	−0·0063	0·342
In(3L)P	−0·409	−0·319	−0·822***	$-1{\cdot}8\times10^{-4}$	−0·0121	−0·0143***	0·739
In(3R)P	−0·214	−0·356	−0·415	$-1{\cdot}9\times10^{-4}$	−0·0210	−0·0054	0·289
In(3R)K	−0·008	−0·261	−0·581**	$+1{\cdot}4\times10^{-4}$	−0·0027	−0·0149*	0·378
In(3R)C	−0·271	+0·129	−0·143	$-1{\cdot}0\times10^{-4}$	+0·0029	−0·0013	0·082
In(2R)Ca	−0·419	−0·387	−0·513*	$-1{\cdot}8\times10^{-4}$*	−0·0134*	−0·0025	0·517

Simple correlation (*r*) and multiple regression (*b*) coefficients. R^2 is the proportion of variance in inversion frequency explained by the *b* values. Frequencies were angularly transformed.
Abbreviations: *, $p < 0{\cdot}05$; **, $p < 0{\cdot}01$; ***, $p < 0{\cdot}001$.

inversions were pooled and reported as 'unique endemics'. Third, published descriptions and photographs of many inversions were inadequate for their subsequent identification, and different authors often described as identical what were clearly different inversions, and *vice versa*. Thus, the data in Table 5 mainly provide an indication of the world frequency of unique endemics. The five regions considered are (1) tropical Africa, (2) Europe and North Africa (France, Greece, Spain, Canaries, Morocco, Tunisia and Egypt), (3) America (North and Central America), (4) Asia (India, Japan and Korea) and (5) Australasia (Australia, New Guinea and Tasmania). No significant difference exists for Australasia compared to the other regions, which could be a consequence of the number of haplotypes available. The lowest, and significant, frequency (0·8%) is encountered in Europe and North Africa compared to those in America, Africa and Asia. The highest value, although not significantly different from that obtained for Africa, is found in America, where 2·5% of genomes harbour unique inversions.

4. Discussion

Up to now the *D. melanogaster* populations of the Afrotropical region have remained poorly investigated for their chromosomal polymorphism, despite the fact that they correspond to the ancestral populations of the species. The present study fills this gap only partially, because only about 1000 haplotypes have now been analysed, against more than 30,000 in the other parts of the world. However, our data provide several new observations: (1) a large amount of geographic differentiation for polymorphic inversions; (2) the occurrence of six polymorphic endemics specific to Africa; and (3) some longitudinal but no altitudinal nor latitudinal trends, except for the most widespread African polymorphic endemic inversion *In(2R)Ca*. These results need to be considered, as does the role of human activities in explaining the present distribution of genetic markers and the modalities of world colonisation.

(i) *Classification of inversions according to frequency and geographical distribution*

We suppose that, whatever the factors causing chromosomal breaks, each polymorphic inversion probably has a unique origin (Krimbas & Powell, 1992; Lemeunier & Aulard, 1992; Powell, 1997). This hypothesis has been strengthened by molecular studies. The more direct evidence comes from the work of Wesley & Eanes (1994) and Andolfatto *et al.* (1999).

Unique inversions might be found occasionally, in one or a few copies in one population. They are probably newly arisen inversions that have not yet had time to become polymorphic, if they are advantageous; if deleterious, they probably will be lost (Mettler *et al*, 1977). As for allozymes (Lewontin, 1974), when the frequency exceeds 1%, inversions could be considered to be potentially involved in adaptive polymorphism, maintained by selection. As stated in the Introduction, there is a lot of indirect evidence for the adaptive significance of the four common cosmopolitan inversions.

Such a simple situation is, however, complicated by two factors. One is the occurrence of rare cosmopolitans and 'quasicosmopolitans' (Inoue & Igarashi, 1994), which, although observed in various parts of the world, reach neither a high frequency nor a wide distribution. The other is the evidence of polymorphic region-specific endemics, some of which are widespread and reach locally fairly high frequencies in Africa. The simple discrimination between rare endemic deleterious variants and positively selected polymorphic inversions is obviously not a clear-cut one, with many possible transitions.

If we consider the six classical rare cosmopolitans (Lemeunier & Aulard, 1992), four have been detected in Africa. Two of them are very rare (*In(2L)NS* and

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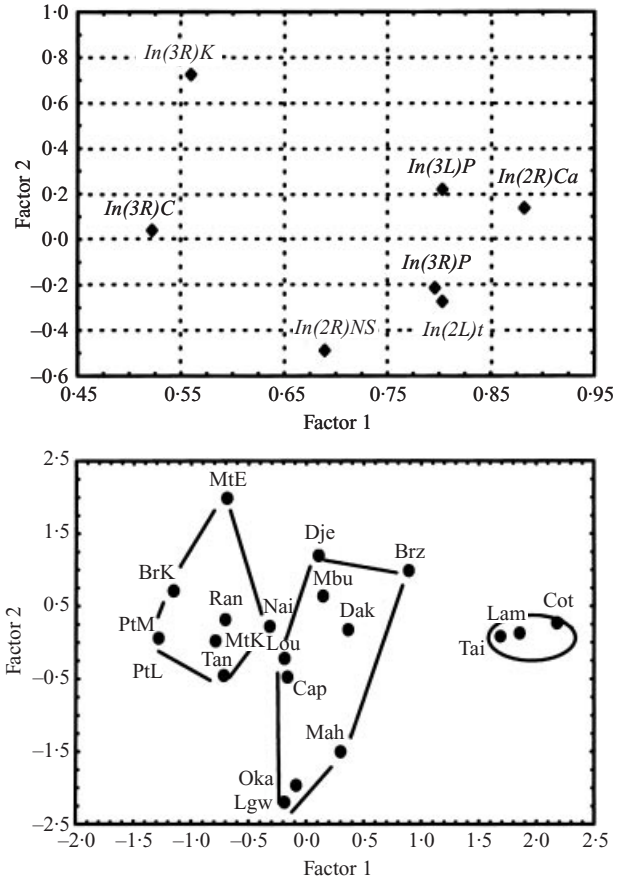

Fig. 4. Principal components analysis of the *D. melanogaster* African populations. The first two principal components reflected 54% and 14% of the total variability, respectively. Correlations between inversions and the principal components (top) and scatter plots of the African populations (bottom) are shown, after angular transformation of frequencies. The first axis (factor 1) helps to distinguish three groups of populations: low polymorphism (left), moderate polymorphism (middle) and high polymorphism (right). Abbreviations: BrK, Brazzaville–Kronenbourg; Brz, Brazzaville; Cap, Cape Town; Cot, Cotonou; Dak, Dakar; Dje, Djeffa; Lam, Lamto (1984); Lgw, Luangwa; Lou, Loua and Loukanga; Mah, Mahe; Mbu, Mbuluzi; MtE, Mt Elgon; MtK, Mt Kenya; Nai, Nairobi; Oka, Okavango; PtL, Port Louis; PtM, Port Mathurin; Ran, Ranomafana; Tai, Tai (1981 and 1983); Tan, Tananarive.

In(3R)Mo), whereas the two others have been found in many populations, especially *In(3R)K*, which has been encountered in 66% of the samples (Table 2) with frequencies of up to 0·48 (Table 1).

The occurrence of six polymorphic endemic inversions is a specific feature of Afrotropical populations. These inversions are spread over different countries and four of them can reach frequencies above 0·10 in local populations (Table 2). Again, these rearrangements should be included in the polymorphic system and, in this respect, we can conclude that Africa is qualitatively more polymorphic than the rest of the world. Other polymorphic endemics have already been observed, especially in Asia (Inoue & Igarashi, 1994), but usually at low frequency and never over a large area. In our opinion, in addition to the African ones, only five inversions (*In(2L)A*, *In(2L)W*, *In(2R)O*, *In(3L)L* and *In(3L)Y*) meet the definition of polymorphic endemics (Lemeunier & Aulard, 1992). Among the six polymorphic endemics found in Africa, one (*In(2L)IC*) might be 'quasicosmopolitan', because a similar inversion (*In(2L)KA*) also exists in Korea (Paik, 1979; Choi *et al.*, 1984), Japan (Inoue & Igarashi, 1994) and possibly Brazil (dos Santos *et al.*, 1991). However, the absence of any photograph makes it difficult to ascertain the breakpoint's identity.

If we now come back to the rare endemic inversions, the situation is not so clear (but see the comments in section 3). 18 have been found (Table 5). If we assume that these inversions depend on the mutation–selection balance, more might be expected in Africa because of a higher effective population size, in agreement with the ancestral status and a long-established demographic equilibrium. However, the number observed in Africa is only significantly different from India, Korea and North Africa. The highest frequency is observed in America and, in this case, a higher mutation rate might be the explanation. For example, rearrangements induced by the P transposable element should be more frequent because this transposon probably first invaded the American populations in the recent past (Anxolabéhère *et al.*, 1988). The P or

Table 5. *Frequencies of unique autosomal inversions in different geographical areas*

	Geographical area	*N*	*n*	%	Ref
a	Africa	953	18	1·89	1
b	America	7498	188	2·51	2
	Mexico	*1586*	*28*	*1·77*	
	North	*5912*	*160*	*2·71*	
c	Australasia	626	9	1·44	3
d	Asia	18551	235	1·27	4
	India	*3216*	*18*	*0·56*	
	Japan	*10046*	*163*	*1·62*	
	Korea	*5289*	*54*	*1·02*	
e	Europe/North Africa	7392	59	0·80	5
	Europe	*2682*	*37*	*1·38*	
	North Africa	*4710*	*22*	*0·47*	
	Total	35020	509		

Abbreviations: *N*, number of genomes analysed; *n*, number of unique inversions recorded.
References: 1, present study; 2, Yang & Kojima, 1972; Pipkin *et al.*, 1976; Stalker, 1976; Mettler *et al.*, 1977; 3, Knibb *et al.*, 1981; 4, Choi, 1977; Paik, 1979; Choi *et al.*, 1984; Inoue, 1988; Singh & Das, 1990; Das & Singh, 1991; 5, Mourad & Mallah, 1960; Zaccharopoulou & Pelecanos, 1976; Masry, 1981; 1984; 1986; Roca *et al.*, 1982; Afonso *et al.*, 1985; Aulard & Lemeunier, 1985; Aulard, 1986; Taberner & Gonzales, 1991.
Significant χ^2 contingency tests: $p < 0{\cdot}001$ for a vs e, b vs d and b vs e; $p < 0{\cdot}01$ for d vs e.

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hobo transposable elements have been suggested to have roles in the origin of inversions (Kusakabe *et al*., 1990; Lyttle & Haymer, 1992; Zabalou *et al*., 1994; Ladevèze *et al*., 1998). However, very little is known about the implication of transposable elements in the occurrence of inversions in nature and their activity is probably not the only factor involved.

(ii) *Geographic variations of polymorphic inversions*

Polymorphic inversions, and especially common cosmopolitans, are involved in various selective processes. This is demonstrated beyond any reasonable doubt by many observations outside Africa, such as parallel latitudinal clines on different continents and cyclic seasonal variations. *Standard* sequences seem to be favoured in colder places or during the cold season, whereas inversion frequency increases according to ambient temperature and rainfall. The exact nature of the selection process is, however, still unclear (van Delden & Kamping, 1997).

Our African results do not fit this general tendency, because no latitudinal nor altitudinal trends have been found for any rearrangement, except the African *In(2R)Ca* (Table 5). However, it is possible that some 'local' clines exist, but the samples are much too dispersed to reveal them. Unlike the African populations, latitudinal clines were found in the USA and Australia for populations distributed along a transect. Moreover, the African samples were recorded in much more heterogeneous habitats. Significant variation has, however, been observed and might be described as long-range, medium-range and short-range variation.

The present day distribution of *D. melanogaster* shows a striking West–East differentiation (Lachaise *et al*., 1988). Similarly, long-range analyses of inversion polymorphism have shown a major longitudinal effect, permitting a subdivision of our populations into three groups: a highly polymorphic western group; a central group with an intermediate level of polymorphism; and an eastern group with the lowest polymorphism. An interesting observation is the positive correlation between inversions: populations that are highly polymorphic are so for all chromosomal arms, an observation that is also valid in other parts of the world. We cannot, however, correlate these variations in Africa with a climatic or some other ecological trend, nor suggest any adaptive interpretation.

Medium-range variation, between sites separated by a few hundreds of kilometres, has been observed in several cases, for example between Mt Elgon and Mt Kenya. The populations are separated from one another by 300 km of an arid, hot area, the Oriental Rift Valley, which prevents migration. By contrast, there are no such geographical and ecological barrier between Nairobi and Mt Kenya. This can explain the significant differences, for *In(2L)t* and *In(3R)K*, between Mt Elgon and Mt Kenya or Nairobi. Moreover, no significant difference is found between Nairobi and Mt Kenya. The two altitudinal Malagasy samples, Tananarive and Ranomafana ($\sim$ 400 km south of Tananarive), display a low and not significantly different level of polymorphism, rather restricted to the presence of *In(2L)t*. However, a higher level of polymorphism has been detected in a preliminary survey of another sample, collected in 1994 in Tulear (at sea level, 23·21 °S 43·40 °E), southwest of Madagascar (data not shown). The cosmopolitan *In(3L)P*, *In(3R)P*, *In(3R)K* and *In(3R)C* inversions are found there, and indicate that regional differentiation might also occur in Madagascar.

Significant genetic differences over a few kilometres have also been observed in African populations. The best example is provided by field and brewery (Kronenbourg) populations in Brazzaville. In this case, strong, divergent selections seem to occur in different habitats in relation to alcoholic resources (Vouidibio *et al*., 1989; Capy *et al*., 2000). There is no doubt that inversions are related to ecological features (Stalker, 1976; Gonzáles & Ménsua, 1984; Gonzáles & Ménsua, 1987), which might explain the observed polymorphisms. A similar explanation (unpublished observations) might be valid in Benin, for explaining the differences between Cotonou and Djeffa.

Finally, variation in the same locality has been observed over different years (e.g. Tai). The Ivoryan samples display similar polymorphisms but with significant higher frequencies in Tai, in 1981, for *In(2R)Ca* and *In(3L)P*, compared with those observed in 1983. These observations might reflect some seasonal variations: one sample was collected during the wet season (1981), the other during the dry season (1983).

(iii) *Migration and gene flow within Africa*

The geographical distribution of the polymorphic endemic inversions gives prominence to a West–East differentiation that was also observed for molecular variation at the *Adh* locus (Bénassi & Veuille, 1995). Three are restricted to the East: *In(1)A* is found in Tanzania, Zambia and Botswana; *In(3L)Ok* in Kenya, Malawi, Zambia and Botswana; a local diffusion is especially clear for *In(2LR)PL*, found in Mauritius and Rodrigues, for which a unique origin is supported by RLFP analyses (Coyne *et al*., 1991). The other three, which presumably originated in West Africa, are mostly found in the West. The currently available data also strongly suggest, for several of them, long-range migrations. For example, *In(2L)IC* is found in the Ivory Coast and Benin, but also in

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three Indian Ocean islands (La Réunion, Mauritius and Rodrigues); also, *In(2R)Ca* is found in Cameroon, the Ivory Coast, Benin, Gabon and Congo, but also in the Seychelles. In Mauritius and the Seychelles, *D. melanogaster* is rare and is likely to have been introduced quite recently (David & Capy, 1982; David *et al*., 1989; Coyne *et al*., 1991). Morphometric and allozyme data suggest an introduction from a country with a Mediterranean climate such as South Africa (David & Capy, 1982; and unpublished data). Inversions now suggest a multiple foundation, with the help of modern humans.

(iv) *Expansion of D. melanogaster over the world*

David & Capy (1988) suggested three categories of populations: (i) ancestral, that is, Afrotropical populations; (ii) ancient populations in North Africa, Europe and Asia, for which the colonization was a natural phenomenon, prior to the development of modern transportation; (iii) new populations, found mainly in America and Australia. America, at least in its tropical part, was probably colonized several centuries ago, from West African populations. The connection between these populations and those from the USA is supported by molecular analyses at the *Adh* locus (Bénassi *et al*., 1993). There were probably several introductions into the Caribbean islands and the mainland. Concerning Australia, the origin is less clear because we lack convenient genetic markers. Common cosmopolitan inversions, which are widespread over Africa, do not provide reliable information. The rare and quasicosmopolitans might be more informative. Although *In(3R)K* and *In(3R)C* are widespread, *In(2L)NS* and *In(3R)Mo* are rarer in Africa. Outside Africa, *In(2L)NS* is known only from Nova Scotia (Canada) and Egypt, and its frequency is always low. By contrast, *In(3R)Mo*, rarely found in Africa, is known from many places in the world: North and Central America (USA, Mexico), Australia, Asia (India, Japan, Korea), Europe (Italy, Greece, the UK, Austria, Finland, Hungary, Spain, ex-USSR) and Egypt. *In(3R)K*, which is common in Africa, is also reported from North, Central and South America, Europe, and North Africa, but it never reaches a frequency above 0·05. It is rarely found in Japan and has never been observed in Australia. *In(3R)C* presents a geographical distribution similar to that of *In(3R)Mo* but, in contrast to this last inversion, it is also quite common in Africa.

Polymorphic endemic inversions, finally, raise an interesting problem. As seen from Table 2, they are widespread, because most of them have been found in $> 10\,\%$ of the samples. The question is thus why none of them has been exported outside Africa. This might suggest that colonization occurred from places lacking such rearrangements.

In light of all these original features, the total number of haplotypes currently investigated appears to be small and insufficient. Tropical Africa should be chosen as a favourite place for future investigations in *D. melanogaster*. Many areas have not yet been sampled, particularly the central Congo basin, with the Chad–Sudan region to the north and the Angola region to the south.

We thank C. B. Krimbas and M. Veuille for stimulating discussions, C. Barjolin for technical assistance, and all collectors for the *Drosophila* strains. We are most grateful to B. Charlesworth and two anonymous reviewers for helpful suggestions. This work was partially supported by grants from CNRS (ATP, RCP and Ecotrop).

Appendix 1. *Synopsis of African populations considered in the present work*

Country		Locality	Altitude	Latitude	Longitude	Date	Collectors	*N*	Ref.
Senegal	1	Dakar	Sea level	14·40 N	17·26 W	1982		74	e
Ivory Coast	2	Abidjan		5·19 N	4·02 W	1969	L. Tsacas	*	g
	3	Agboville		5·56 N	4·13 W	1972	J. David	*	g
	4	Bouake		7·41 N	5·02 W	1973	G. de Jong	*	g
	5	Tai	100 m	5·52 N	7·27 W	1981	D. Lachaise	42	a
		Tai	100 m	5·52 N	7·27 W	1983	D. Lachaise	75	a
	6	Adiopodoume		5·19 N	4·08 W	1983	D. Lachaise	*	a
	7	Lamto	80 m	6·15 N	5·00 W	1984	D. Lachaise	33	a
		Lamto	80 m	6·15 N	5·00 W	1989	D. Lachaise	83	c
Benin	8	Porto-Novo		6·29 N	2·37 E	1972	G. de Jong	*	g
	9	Cotonou	Sea level	6·21 N	2·25 E	1987	O. Dainou / J. David	36	a
	10	Djeffa	Sea level	6·22 N	2·30 E	1987	O. Dainou / J. David	29	a
Cameroon	11	Kumba		4·38 N	9·25 E	1973	V. Southgate	*	g
Gabon	12	Belinga		1·05 N	13·13 E	1970	J. David	*	g
	13	Libreville		0·23 N	9·27 E	1972	J. David	*	g
	14	Makokou		0·34 N	12·52 E	1970	J. David	*	g
		Makokou		0·34 N	12·52 E	1980	D. Lachaise	*	a
Congo	15	Loua	310 m	4·18 S	15·09 E	1981	J. Vouidibio	60	a
	16	Brazzaville	310 m	4·15 S	15·14 E	1986	J. Vouidibio	42	a

Appendix 1 (*cont.*)

Country		Locality	Altitude	Latitude	Longitude	Date	Collectors	*N*	Ref.
Congo	17	Brz-Kronenbourg	310 m	4·15 S	15·14 E	1988	J. Vouidibio	18	a
	18	Loukanga	310 m	4·20 S	15·09 E	1988	J. Vouidibio	19	a
Uganda	19	Kampala		0·19 N	32·25 E	1973	A. C. Tallantire	*	g
Kenya	20	Mombasa		4·03 S	39·40 E	1980		*	f
	21	Nairobi	1600 m	1·17 S	36·49 E	1980		54	f
	22	Mount Elgon	2200 m	1·05 N	34·45 E	1984	M. A./M. L. C./D. L.	21	a
	23	Mount Kenya	1950 m	0·10 S	37·00 E	1984	M. A./M. L. C./D. L.	30	a
Tanzania	24	Nyengesi-Mwanza		2·31 S	32·54 E	1984	J. van Alphen	1	a
Malawi	25	Limbe		15·49 S	35·03 E	1973	H. R. Feijen	*	g
	26	Kasungu		13·01 S	33·30 E	1991	D. Lachaise	50	b
	27	Lilongwe		13·59 S	33·44 E	1991	D. Lachaise	12	b
Zambia	28	Luangwa	#1000 m	#12·00 S	#32·00 E	1985		86	d
Zimbabwe	29	Mount Silinda		20·25 S	32·43 E	1970	H. Paterson	*	g
Botswana	30	Okavango	#600 m	#18·45 S	#22·45 E	1985		71	d
Swaziland	31	Mbuluzi	300 m	26·10 S	31·50 E	1984	A. Potts	9	a
South Africa	32	Cape-Town	Sea level	33·58 S	18·36 E	1984	J. David	26	a
Seychelles	33	Mahe	Sea level	4·37 S	55·27 E	1985	J. David	34	a
Madagascar	34	Tananarive	1300 m	18·54 S	47·32 E	1980		26	f
	35	Ranomafana	950 m	21·19 S	47·39 E	1987	S. A./J. D./S. F. M.	35	a
La Reunion	36	St Denis		20·52 S	55·28 E	1973	J. David	*	g
Mauritius	37	Port Louis	Sea level	20·10 S	57·30 E	1985	M. Solignac	30	a
Rodrigues	38	Port Mathurin	Sea level	19·41 S	63·25 E	1985	M. Solignac	14	a
Total number of haploid genomes								1010 (+15*)	

Abbreviations: *N*, number of haploid genomes; *, qualitative data; M. A., M. Ashburner; M. L. C., M. L. Cariou; D. L., D. Lachaise; S. A., S. Aulard; J. D., J. David; S. F. M., S. F. McEvey.
References: a, present study; b, Bénassi, 1994 (data only for chromosome 2); c, Bénassi *et al.*, 1993 (data only for chromosome 2); d, Eanes *et al.*, 1992; e, Afonso *et al.*, 1985; f, Inoue & Watanabe, 1980; g, Ashburner & Lemeunier, 1976.

Appendix 2. *Rearrangements identified in D. melanogaster Afrotropical populations*

X Chromosome:

1. *In(1)12A;18D*, recurrent endemic (abbreviated *In(1)A*): Tanzania (Nyengesi), Zambia (Luangwa)[d], Botswana (Okavango)[d]. (19)
2. *In(1)16D;18D*, recurrent endemic (abbreviated *In(1)Be*): Ivory Coast (Tai 1981 & 1983, Adiopodoume), Benin (Cotonou 1981[h] & 1987), Congo (Brazzaville 1986 & Brazzaville-Kronenbourg 1988), South Africa (Cape Town). (14)

Chromosome 2, 2L arm:

3. *In(2L)22A;26B*, recurrent endemic (abbreviated *In(2L)IC*): Mauritius (Port Louis), Rodrigues (Port Mathurin), Ivory Coast (Bouake)[g] Benin (Porto Novo)[g], La Réunion[g]. (5)
4. *In(2L)t22D3-E1;34A8-9*, common cosmopolitan. (315)
5. *In(2L)NS22E2-3;35F5-36A1*, rare cosmopolitan: only found in Ivory Coast (Lamto 1989)[c], in Zambia (Luangwa)[d] and/or Botswana (Okavango)[d]. (4)
6. *Df(2L)30DE;34A*, unique endemic: Benin (Cotonou). (1)

Chromosome 2, 2R arm:

7. *In(2R)41F;51D*, unique endemic: Ivory Coast (Tai 1983). (1)
8. *In(2R)43B;54E+52C;53E*, unique endemic: Ivory Coast (Tai 1981). (1)
9. *In(2R)43CD;55B*, unique endemic: Ivory Coast (Lamto 1989)[b]. (1)
10. *In(2R)44F3-12;54E3-10+51B6-11;55E3-12*, unique endemic: found in two lines from Malawi (Kasungu)[b]. (2)
11. *In(2R)44F3-12;53F6-13*, unique endemic: Ivory Coast (Lamto 1989)[c]. (1)
12. *In(2R)49B;56A*, recurrent endemic (abbreviated *In(2R)Ca*): Ivory Coast (Tai 1981 & 1983, Lamto 1984 & 1989), Benin (Cotonou, Djeffa), Gabon (Makokou), Congo (Brazzaville), Seychelles (Mahe), Cameroon (Kumba)[g]. (26)
13. *In(2R)NS52A2-B1;56F9-13*, common cosmopolitan. (82)
14. *In(2R)53B;55C*, unique endemic: La Réunion[g]. (1)
15. *In(2R)53F;58E*, unique endemic: Rodrigues (Port Mathurin). (1)

Chromosome 2, pericentric inversions:

16. *In(2LR)23B;50F5-9*, with *In(2L)t*, unique endemic: Ivory Coast (Lamto 1989)[b]. (1)
17. *In(2LR)30C;47EF*, unique endemic: Gabon (Belinga)[g]. (1)
18. *In(2LR)31F;51C*, recurrent endemic (abbreviated *In(2LR)PL*): Mauritius (Port Louis), Rodrigues (Port Mathurin). (2)

https://doi.org/10.1017/S0016672301005407 Published online by Cambridge University Press

Appendix 2 (*cont.*)

19. *In(2LR)36D;46F*, unique endemic: Gabon (Belinga)[g]. (1)

Chromosome 3, 3L arm:
20. *In(3L)62DE;68A*, recurrent endemic (abbreviated *In(3L)Ok*): Malawi (Limbe)[g], Kenya (Mombasa)[f], Zambia (Luangwa)[d], Botswana (Okavango)[d]. (46)
21. *In(3L)P63B8-11;72E1-2*, common cosmopolitan. (95)
22. *In(3L)65F;73C*, unique endemic: found in two lines from South Africa (Cape Town). (2)
23. *In(3L)66C;71B*, unique endemic: found in two lines from Benin (Djeffa). (2)
24. *In(3L)66DE;71AB*, unique endemic: Senegal (Dakar)[e]. (1)
25. *In(3L)71A;72EF*, unique endemic: found in two lines from Ivory Coast (Tai 1981). (2)

Chromosome 3, 3R arm:
26. *In(3R)84AC;90*, unique endemic: Senegal (Dakar)[e]. (1)
27. *In(3R)86E;99B*, with *In(3R)P*, unique endemic: Congo (Loua). (1)
28. *In(3R)K86F1-87A1;96F11-97A1*, rare cosmopolitan. (124)
29. *Df(3R)87A;87C*, unique endemic: Mauritius (Port Louis). (1)
30. *In(3R)87B;93F*, unique endemic: Senegal (Dakar)[e]. (1)
31. *In(3R)88E;93F*, unique endemic: La Réunion[g]. (1)
32. *In(3R)P89C2.3;96A18.19*, common cosmopolitan. (141)
33. *In(3R)C92D1-E1;100F2.3*, rare cosmopolitan. (28)
34. *In(3R)Mo93D;98F2.3*, rare cosmopolitan: only found in South Africa (Cape Town). (3)

The total number of observed rearrangements is given in brackets at the end of each line.
References: a, present study; b, Bénassi, 1994 (data only for chromosome 2); c, Bénassi *et al*., 1993 (data only for chromosome 2); d, Eanes *et al*., 1992; e, Afonso *et al*., 1985; f, Inoue & Watanabe, 1980; g, Ashburner & Lemeunier, 1976; h, Chenevix-Trench, 1981.

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